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THE LESSER ANTILLEAN REPRESENTATIVES
OF *BOTHROPS* AND *CONSTRUCTOR*

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No. 3—*The Lesser Antillean Representatives of Bothrops
and Constrictor*

By JAMES D. LAZELL, JR.

The taxonomy of four Lesser Antillean populations of snakes, two of *Bothrops* and two of *Constrictor*, has long been in a state of confusion. This situation is perhaps explicable, as so many similar situations in West Indian herpetology are, because there were until now very few examples of these populations in collections, and there was virtually no record of the animals in life. I have combined in this paper a revision of the Lesser Antillean populations of the two genera because their zoogeography is quite comparable, while their taxonomy presents two very different patterns of differentiation in island forms.

BOTHRUPS

Bothrops has been erroneously recorded from numerous islands in the Lesser Antilles. Barbour (1914) pointed out that, in the Lesser Antilles proper, members of this genus occur only on Martinique and Saint Lucia. Lacépède (1789) described the Martinique serpent and concocted the name "Fer-de-lance" himself, stately (pp. 121-122) because he did not particularly like the vernacular name "Vipère jaune." It is interesting to note that many authors (e.g. Ditmars, 1954) have attributed the use of the term "Fer-de-lance" to the natives of Martinique, Saint Lucia, or both; the term "Fer-de-lance" is not the vernacular name of any reptile occurring in any French or Creole-speaking country in the New World, and *Bothrops*, on both Martinique and Saint Lucia, is known merely as "Serpent."

Lacépède cited a specimen of his *Coluber lanceolatus* (Tables, p. 80) from Martinique with 228 ventrals, and mentions a second (p. 126) that had 225 ventrals. These figures unequivocally assign the name to the Martinique form: no other member of the genus *Bothrops* that has divided subcaudals can equal such high ventral counts.

Amaral (1925) differentiated three sympatric species of *Bothrops* from Brazil: *atrox*, *jararaca*, and *jararacussu*. At the same time he placed *lanceolatus* in the synonymy of *atrox*. The three sympatric species he differentiated (pp. 41-43) do not differ

absolutely on any character of squamation — except that *jararacussu* is implied to have a divided anal constantly. Amaral said also (p. 22), “color characteristics, . . . of course, are among the main points on which . . . specific differentiation can be based.” Unfortunately, Amaral apparently failed to note that the dorsal pattern of the Saint Lucian specimens he examined was absolutely distinct from any of the other forms.

Hoge (1952) attempted to revalidate the name *lanceolatus* for the Martinique form. He believed that the number of scale rows around the middle of the body, the number of ventrals, the structure of the hemipenes, the carination, and the coloration of the Martinique form justified its recognition as a distinct species.

Amaral (1954) stated that none of Hoge’s arguments “resists . . . scientific analysis.” To be sure, the color characters cited by Hoge are not those which are distinctive: Hoge did not mention the unblotched venter. Also, to date, no one has been able to make taxonomic sense out of the remarkable variants in carination that appear in the South American snakes referred by Amaral to *atrox*; some of these do match the condition of carination found in Martinique specimens. I have not seen sufficient material of properly prepared hemipenes to be able to refute Amaral’s rejection of this character, though there certainly appear to be differences between Martinique and mainland specimens that I have examined.

With respect to squamation, Amaral’s method of “scientific analysis” consisted of lumping together *all* of the “island populations” (Martinique, Saint Lucia, Trinidad, and “Tobago”), and pointing out that this composite was not distinctive from his concept of *Bothrops atrox*. An “analysis” such as this admirably succeeds in obscuring real differences, and *Bothrops lanceolatus* was once again returned to synonymy of *atrox*.

The specimens Amaral examined from “Tobago” agreed with Martinique material in dorsal and ventral counts, and Amaral felt that this fact alone was enough to deprive the Martinique Serpent of taxonomic rank, since those from the geographically intermediate island of Saint Lucia agreed with Trinidad material. This presented a situation that Amaral could not make agree with his concepts of taxonomy and zoogeography: recognition of the Martinique form would be “impossible, in the light of our present knowledge of the phenomena of speciation among ophidians.”

As Dunn (1934a) pointed out, the Lesser Antilles give every appearance of random population by "waifs." In such cases one can hardly expect distribution patterns to be orderly. Furthermore, unless "ophidian" is to be taken here as excluding the possibility of comparable phenomena in, for example, saurians, the situation with respect to the distribution of the two species of *Iguana* in the Lesser Antilles (Dunn, 1934b) may be taken as an excellent precedent for the sort of pattern Amaral thought he was seeing. There is, therefore, no possible recourse in either speciation or zoogeography — as these fields are known now, or as they were known in 1934 — that can support Amaral's contention.

As a matter of fact, however, I have personally collected in Tobago, and I am quite sure there are no *Bothrops* there; nevertheless, for confirmation, I wrote to Arthur Greenhall, Royal Victoria Institute, Port of Spain, Trinidad. Greenhall replied (pers. comm.): "I have done some checking for you on *Bothrops* and can find nothing here to indicate that *Bothrops* or Fer-de-lance or for that matter any highly venomous snake occurs on Tobago or has ever been recorded from Tobago. Tobagonians make no reference to any poisonous snakes on the island."

I have examined two specimens of *Bothrops* in the United States National Museum (USNM) collected by F. A. Ober in 1878 and labelled "Tobago": USNM 10116, a male, has 31 dorsal scale rows at midbody, 218 ventrals, and three rows of suboculars; USNM 10122, a female, has 33 dorsal scale rows at midbody, 231 ventrals, and also three rows of suboculars. These specimens appear, therefore, to be those on which Amaral's remarks were based. Also collected by Ober in 1878 and labelled as coming from "Tobago," is a series of typical *Anolis roquet roquet*, *sensu stricto*, USNM 10102-12. These anoles occur only in Martinique. It is therefore not surprising that the two supposed "Tobago" *Bothrops* agree in every respect of coloration and pattern, as well as squamation, with the Serpent of Martinique, *Bothrops lanceolatus*. If these specimens are, in fact, those Amaral referred to, then we need not give further consideration to a Tobagonian population: the locality is simply in error.

Garman's (1887) *Trigonoccephalus caribbaeus* has been almost universally ignored. The name is available for the St. Lucian *Bothrops*, but the tendency has been that when *lanceolatus* was lumped with *atrox*, *caribbaeus* went with it, though with con-

siderably less ceremony. On the basis of Garman's description, the beast is indeed not separable from *B. atrox* of South America, and it was Boulenger (1896) who first synonymized it in his composite concept of *B. lanceolatus*.

My own re-evaluation of the taxonomy of these forms is based on fresh material of precisely known provenance from both islands (see Tables 1 and 2). Although I do not have the number of specimens that Amaral claimed to have had from Martinique, I do at least know that the specimens I report on here actually came from Martinique, for I collected them myself. With respect to Saint Lucia, however, I collected twenty specimens myself (nearly three times the number examined by Amaral) and have since removed twenty-six young from one of the larger females of this series — making in all forty-six specimens.

The two *Bothrops* populations — Martinique and Saint Lucia — are absolutely distinct from each other on the basis of color, pattern, squamation, habits, and habitat. However, differentiating either of them from *B. atrox* of South and Central America seemed at first an almost impossible task: *B. atrox* as currently conceived is so remarkably variable, often with respect to those characters that are most constant in the island forms, that many of the differences I at first thought valid crumbled before the sheer number of preserved *atrox* I examined. It was not until I began using a combination of characters that I was able to define the Lesser Antillean forms unequivocally.

I regard both island species as distinct not only from each other but also from their relatives on the continent. A full discussion of why I regard them as distinct species rather than as geographic races of one of the South American forms will be presented below. The closest population of *Bothrops*, geographically, to a Lesser Antillean form is *B. atrox* of Trinidad; thus, discussing the populations in order of geographic proximity to their closest neighbor, the first is:

BOTHIROPS CARIBBAEUS (Garman)

Trigonocephalus caribbaeus Garman, 1887, Proc. Am. Phil. Soc., 24: 285.

Lachesis lanceolatus (part), Boulenger, 1896, Cat. Snakes Brit. Mus., 3: 535-537.

Bothrops atrox (part), Amaral, 1925, Contr. Harvard Inst. Trop. Biol. Med., 2: 22-43.

Lectotype: Here designated as MCZ 4814, "St. Lucia," S. Garman, collector.

Type locality: Here restricted to Grande Anse, Saint Lucia.

Diagnosis. A *Bothrops* with divided subcaudals, 25 to 29 dorsal scale rows at midbody, 7 or 8 supralabials, 9 to 11 infralabials, 2 rows of scales between the eye and the supralabials, and 198 to 212 ventrals; venter yellow to cream-colored, sometimes finely peppered with grey laterally but never blotched or mottled; an irregular, dull, dark stripe from the eye passes well dorsal to the commissure of the mouth and never crosses the infralabials; dorsal pattern best developed middorsally, vague or nonexistent laterally; dark dorsal markings with borders that are parallel or diverging at middorsum.

Color. The ground color is usually grey (concrete-colored) to grey-brown; the markings vary from slate grey, on the paler, concrete-colored specimens, to chocolate on the darker ones. A common variant is yellowish ground color with rust-reddish markings. Males are much darker generally than females and

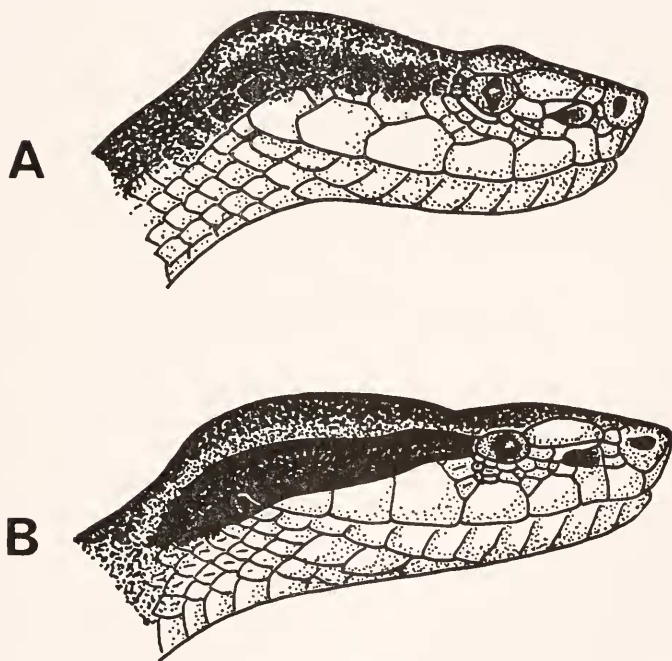


FIG. 1. Heads of two species of *Bothrops*. A, *B. caribbaeus* (Garman), Lectotype, MCZ 4814, Saint Lucia; B, *B. lanceolatus* (Lacépède), MCZ 75839, Morne Capot above Lorrain, Martinique.

sometimes have a slightly olive tint. The belly is always yellowish, though the chin is white, or, on those with the yellowest bellies, cream-colored. Some specimens, e.g. MCZ 70211, are very reddish — brick red to russet. Most specimens, of either sex and at any age, have "rust marks" on the face; these marks have remarkably the same appearance as the stain left on concrete by a rusting nail and are not arranged in any particular pattern — even varying on the two sides of the same snake.

Perhaps the most striking field mark is the dark temporal stripe. This stripe is usually present in *Bothrops* and passes from the eye across the temporal region onto the neck. In *Bothrops caribbacus* this stripe is dull and irregular, rather than glossy and sharply defined; in addition, it passes well dorsal to the commissure of the mouth and does not involve any infralabials. This condition is shown in Figure 1A.

The dorsal pattern is immediately distinctive. The dark markings may alternate or coincide but are always well defined at the middle of the dorsum and generally extend across the middorsum, even when alternate. The markings are broad (at least 40% of the distance between them), and the borders are always either parallel or diverging at middorsum.

Amaral (1925, pl. IV, fig. 1) shows a figure supposedly of MCZ 4815 — a juvenile collected by Semper. In this figure the dorsal markings, as in *B. atrox* and its mainland relatives, converge towards the middorsum. Fortunately, I have MCZ 4815 before me and can state emphatically that the drawing is incorrect on this point: the specimen is a typical *caribbacus* with respect to its dorsal pattern, and the borders of the markings are sometimes parallel, sometimes diverging, at the middorsum.

Habits and habitat. Compared to the Serpent of Martinique, or presumably to *Bothrops insularis*, this form is only semi-arboreal at best. Most of the specimens I collected were in rock piles or coconut husk piles. They do, however, climb frequently and are very often encountered in trees. The greatest height at which I collected one was six meters from the ground (MCZ 70210). *Bothrops caribbacus* feeds to some extent on birds, but the introduced rats and mongooses seem to have earned a good deal of their present attention. In areas where *Bothrops* are plentiful there is said to be virtually no rat damage to such crops as cocoa; in parts of the island where there are no *Bothrops*, crop damage to cocoa is said to run as high as 70 per cent.

When cornered, *Bothrops caribbaeus* often shows a feeble tendency towards tail vibration and generally inflates the throat; if the throat and chin were yellow, this would produce the "yellow beard" that has presumably resulted in the vernacular name — "barba amarillo" — given to *B. atrox* in some parts of its range.

Range. *Bothrops caribbaeus* is confined to the coast and elevations under 200 meters. It occurs along both the windward and the leeward coasts and across the island in the north from the area of Grande Anse and Marquis to slightly north of Castries. The range (see Figure 2) is thus sharply U-shaped and covers

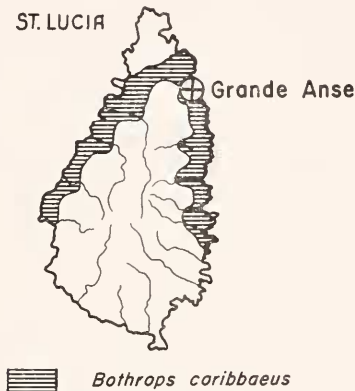


FIG. 2. Saint Lucia, showing the range of *Bothrops caribbaeus*.

the moderately dry lowlands of the island. Serpents are absent from the extremely dry north tip (Cap Estate), from the southern and central highlands and, rather inexplicably, from the entire south coast. The only place where man seems to have had any real effect on their abundance is in the vicinity of Castries; nevertheless, I got some reports of Serpents recently seen quite close to town. Elsewhere in its range the Serpent of Saint Lucia is plentiful compared to most North American snakes with which I am familiar (e.g. *Thamnophis sirtalis*). In some areas (e.g. Grande Anse) the Serpent is abundant almost beyond belief.

Size. The largest specimen I collected measured 1,545 mm (MCZ 70204). A larger specimen represented only by the

mangled carcass, from Marquis, was two meters without the head. There are a number of reasonable reports of individuals that were roughly "seven feet" (over two meters). They certainly average much smaller than do Serpents from Martinique; the average size of the twenty specimens I collected (the twenty-six young are not included) was about one meter.

Relationships. With respect to dorsal and ventral scale counts *Bothrops caribbaeus* does not differ from either *B. atrox* or *B. jararaca*. The incidence of 8 supralabials is 15 per cent; this is intermediate between the two latter species. The dorsal pattern, with transverse markings whose borders are parallel or diverging at middorsum, can be matched by some *Bothrops insularis*. A character which Amaral (1921, p. 80) mentions as being "not found either in *L. jararaca* or *L. atrox*" is the presence of three plate-like scales on the top of the snout; this condition is common in both *B. insularis* and *B. caribbaeus*, though not constant in either.¹

Bothrops caribbaeus and *B. lanceolatus*, of Martinique, have in common their characteristic ventral pigmentation (never blotched or mottled). Both share their arboreal, bird-eating habit with *B. insularis*.

I would suspect that *B. caribbaeus* was derived from the same stock as *atrox* and *jararaca*, and that its differentiation has paralleled that of *insularis*. There is no population both geographically and morphologically intermediate between *B. caribbaeus* and the South American forms, and *caribbaeus* is not at all intermediate morphologically between the South American forms and *B. lanceolatus* of Martinique. *Bothrops caribbaeus* seems certainly to possess an evolutionary role uniquely its own and cannot be interpreted to represent a geographic race of any other species on the basis of either geographical or morphological grounds.

The second population in geographic sequence is, of course, the Serpent of Martinique:

BOTHRUPS LANCEOLATUS (Lacépède)

Coluber lanceolatus Lacépède, 1789, Hist. Nat. Serpens, 2: 80.

Lachesis lanceolatus (part), Boulenger, 1896, Cat. Snakes Brit. Mus., 3: 535-537.

¹ The following paratypes, for example, of *insularis* could not be distinguished from *atrox* with respect to this character alone: MCZ 17620-2 and MCZ 17625.

Bothrops atrox (part), Amaral, 1925, Contr. Harvard Inst. Trop. Biol.

Med., 2: 22-43; Amaral, 1954, Mem. Inst. Butantan, 26: 207-214.

Bothrops lanceolatus Hoge, 1952, Mem. Inst. Butantan, 24(2): 231-236.

Type: Jean Guibé, Muséum National d'Histoire Naturelle, reports (pers. comm.) that the Lacépède specimens apparently no longer exist. Because the characters cited by Lacépède render the allocation of the name unequivocal, I do not feel it necessary to designate a neotype.

Type locality: Here restricted to Morne Capot, between Ajoupa-Bouillon and Lorrain, Martinique.

Diagnosis. A *Bothrops* with divided subcaudals, 9 to 33 dorsal scale rows at midbody, 7 or 8 supralabials, 10 or 11 infralabials, 3 (70%) or 2 (30%) rows of scales between the eye and the supralabials, and 218 to 237 ventrals; venter white, sometimes finely peppered with grey laterally but never blotched or mottled; a sharply delineated, dark, black-bordered, glossy stripe from the eye to the commissure of the mouth, continuing to include at least part of the last infralabial; dorsal pattern of broadly U-shaped dark markings, well accentuated laterally, with borders that converge towards, but are often obscure or obliterated at, the middorsum.

Color. Young specimens are a rather warm grey-brown marked with dark grey; males retain this hue basically but become darker with age and, as adults, may be quite chocolate-brown with a reddish tinge laterally. Young specimens and males are referred to as either "Serpent jaune" or "Serpent rouge," regardless of what color they may appear to the exoteric. The females become gradually greyer, eventually losing all of the brown in the ground color and even the pinkish lateral tinge. They do, however, retain their patterns more boldly than do the males and, because of the crescentic markings, are called "Serpent croissant." The venter is always a virtual dead-white and quite without the mottlings and blotches characteristic of *B. atrox*.

There is a very bold, dark, temporal stripe, passing from the eye to the commissure of the mouth and onto the side of the neck. This stripe is sharply defined, in strong contrast to the surrounding coloration, and *shiny* or glossy in appearance in life. A large portion of the last infralabial is always included within this stripe. This condition is shown in Figure 1B.

Habits and habitat. *Bothrops lanceolatus* is markedly arboreal; it seems especially to prefer the masses of vine that form

interrupted canopies along the edge of the forest and may ascend to twenty meters above the ground. Very large and gravid females are often encountered on the ground and in rock piles, and other specimens may be collected in very steep, rocky hillsides on occasion. This species, because it lives in the better forested regions and in the highlands, is of much less economic value as a rat destroyer than is *B. caribbaeus*. They definitely do eat mongooses, and the larger ones are quite large enough to eat *Didelphis*, which they reportedly do. I suspect, from the type of habitat in which they are usually encountered, that they feed largely on birds, at least until they are too large to move around effectively in the tree tops.

I never saw a specimen either attempt tail vibration or inflate the throat at all, no matter how irritated. Large females are rather lethargic — to the point of docility; males, on the other hand, are fast and aggressive; for this reason the "Serpent jaune" is regarded by most Martinicans as being far more deadly than the other "varieties" they recognize.

Range. In direct contrast to the Serpent of Saint Lucia, this species is confined to wetter regions: highlands, and the well forested coast in the extreme north of the island of Martinique. The range, therefore, appears to be discontinuous. One population occurs in the highlands above Fort-de-France and northward in the mountains to the Montagne Pelée massif and also along the coast in wet regions: i.e. the north tip and the northern windward coast. The other population is confined to the southern highlands: from the region of Morne Serpent and Morne Vauclin southward and westward to the hills between Trois Ilets and Les-Anses-D'Arlets. The people in the central lowlands of Martinique maintain that there are no Serpents there at all. (See Figure 3.)

Size. The largest specimen I collected (MCZ 75836) was two meters long. This form seems to average much larger than *B. caribbaeus*: the average of eight specimens collected was over 1.5 meters. An estate manager from the area of Morne Rouge told of measuring a dead one killed by his workers some years ago that was "two centimeters less than three meters long;" I am inclined to believe this. Specimens in the two-meter range are very easily come by.

Relationships. This form is a bit harder to place than *B. caribbaeus*. The unblotched venter and the frequency of eight supralabials (ca. 33%) are the most evident links between

caribbaeus and *lanceolatus*. In other respects, however, they seem far more different from each other than either is from *atrox* or *jararaca*. Only *B. atrox* from Central America and Mexico can approach *lanceolatus* in squamation; I can, however, find no specimen of either form that is really equivocal with respect to squamation and, in any event, the ventral pigmentation is absolutely different. In short, I think the approach to *lanceolatus*-type squamation in Mexican *atrox* is not an indication of any relationship between the two species: if this situation obtained in Trinidad and Saint Lucia I would be very much more impressed with its value as an indication of relationship, but it does not.



FIG. 3. Martinique, showing the range of *Bothrops lanceolatus*.

Bothrops lanceolatus may be a very much older form than *Bothrops caribbaeus*; in any case, there is no species or group of species (short of all *Bothrops* with divided subcaudals) to which it seems especially allied.

Discussion. The wealth of misinformation that has been perpetuated concerning the Lesser Antillean *Bothrops* populations requires some comment.

Amaral's (1925) lumping of *atrox* and *lanceolatus* is very difficult to explain. *Bothrops lanceolatus* is more different from

atrox with respect to more characters than are either of the two species (*jararaca* and *jararacussu*) which Amaral simultaneously (1925) differentiated from *atrox*. I do not have any means of commenting on Amaral's Martinique specimens, except to say that the scale counts given by Amaral are altogether in keeping with *Bothrops lanceolatus*. Garman (1887, p. 285) gives the minimum ventral count for this form as 217; Amaral lists 218. Garman's figure presumably came from an MCZ specimen, and there is one, MCZ 4817 — a male *lanccolatus* from Martinique — which has 218, as correctly counted by Amaral. This is at best a minor point.

Why *Bothrops caribbaeus* has so long gone unmentioned, and, worse, unsuccessfully differentiated from *B. lanccolatus*, may perhaps be explained by the previous paucity of material. However, all the variant patterns figured, described, and available to me for examination, that appear in *Bothrops atrox* and *B. jararaca*, fail to match the pattern of the Saint Lucian Serpent. It would seem to me that even one specimen would stand out in strong contrast, yet Amaral saw seven and failed to note the differences.

Most remarkable, to anyone who ever actually collected on either Martinique or Saint Lucia, are the statements that one encounters concerning the rarity or even extinction of these Lesser Antillean populations. The earliest one I can find is Amaral (1923, p. 97): "In Martinique Island they introduced mongooses to kill snakes, and they succeeded in extinguishing them, but the country is very small." Compared to Brazil, Martinique is small indeed, but the mongooses have apparently lost ground in the forty years which have elapsed since Amaral made this statement.

In Martinique and Saint Lucia, *Bothrops*, being essentially backward and illiterate, seem unable to distinguish mongooses from other small animals (e.g. rats), and therefore eat them with relish; perhaps, rather than trying to exterminate Serpents directly, it would be easier to merely educate them to the level of those who have pointed out their proper role with respect to mongooses: then the situation would presumably reverse itself.

As my collections of a few weeks suggest, the Lesser Antillean representatives of *Bothrops* have been there much longer than either men or mongooses; it seems to me that they will remain.

Barbour (1914, pp. 230 and 343) discusses the occurrence of *Bothrops* in the Grenadines, pointing out that the island of

Petite Martinique "received its name . . . on account of the abundance of Fer-de-lance there." Actually, this is a nomenclatural problem: the snake responsible for the name of the island is the "Serpent," and the "Fer-de-lance" was never mentioned by anyone except Lacépède, who is alone responsible for this term. In Martinique and Saint Lucia, as I have mentioned, the name "Serpent" refers to *Bothrops*, and only to *Bothrops* (never, for example, to *Constrictor*—which is referred to as the "Tet'chien"—or *Dromicus*, which is called "Couleuvre"). Throughout the Grenadines and in Grenada, however, the arboreal representative of the genus *Boa* is invariably called "Serpent" too; thus, while from the native point of view the woods are full of "Serpents," the term means entirely different things in each area. It is a confusion easily understood by anyone familiar with the habitus and temperaments of Lesser Antillean *Bothrops* and *Boa*.

CONSTRICTOR

The genus *Constrictor* is also known at present from only two islands in the Lesser Antilles. It occurs on Saint Lucia, with *Bothrops*, and on Dominica. Three specimens in the MCZ were received from the New York Zoological Society; two of these, MCZ 6710-11, have no data; the third (MCZ 6659) was supposedly taken on "St. Kitts." All three are typical specimens of the Saint Lucian population. A single specimen collected by Garman (MCZ 6106) represented the Dominican form. During 1958 and 1959 I collected extensively in Dominica and sent a number of *Constrictor* to the Philadelphia Zoological Gardens, as well as to the MCZ; subsequently, some of those sent to Philadelphia died and have been placed in the MCZ. During 1962 I collected in Saint Lucia and placed seven specimens of the *Constrictor* from that island in the MCZ. All MCZ specimens are tabulated (Tables 3 and 4).

The nomenclatural problem in this genus is not, perhaps, less muddled than it was in *Bothrops*, but it is certainly easier to untangle. There is only one South American species, and its nominate subspecies, *Constrictor constrictor constrictor*, is the one closest geographically to the Lesser Antillean forms, occurring both in Trinidad and Tobago. As opposed to *Bothrops atrox*, which I cannot effectively define in relation to the other species in the genus (except to define the others, and then merely say that anything not fitting those definitions is a "*Bothrops atrox*"),

C. c. constrictor may be defined for comparative purposes as follows:

Constrictor constrictor constrictor has a slightly prominent snout and a straight or nearly straight canthus; there are 81 to 95 dorsal scale rows at midbody, 234 to 243 ventrals, and 15 to 22 rather neat, geometric, dark dorsal saddles to the level of the anus; the dorsal ground color is fawn-brown to tan; the venter white to yellow with little dark marking; a dark stripe proceeds from the eye directly to the supralabials (subocular stripe), and a second proceeds from the eye anteriorly in the loreal region, then curves down onto the supralabials (loreal stripe); both stripes correspond to two dark blotches on the infralabials and chin. (See Figures 4 and 5.)

The oldest available name for a Lesser Antillean form is *Boa orophias* Linnaeus (1758); the ventral count given unequivocally assigns the name to the Saint Lucian form since no other member of the genus has 281 ventrals. Duméril and Bibron (1844) applied the name *diviniloqua* to a Saint Lucian specimen; this name was originally proposed by Laurenti (1768). Therefore, *diviniloqua*, *sensu* Duméril and Bibron, is a junior synonym of *orophias*; *diviniloquus*, *sensu* Laurenti, does not seem to apply to any Lesser Antillean form, though, of the two (the Saint Lucian or the Dominican), it could only have applied to *orophias*. No name has ever been proposed for the Dominican form, and the few available specimens have always been considered under *orophias*. Stull (1935) combined both Saint Lucian and Dominican forms under *orophias* and separated this composite from *constrictor* at the species level.

The analogous zoogeographical situation is clear: in *Bothrops* and *Constrictor* there are continental forms which occur also on Trinidad (and, in *Constrictor*, on Tobago too); there is a population far to the north on Saint Lucia in each case, and a third population even farther north, in the case of *Constrictor* on Dominica. The taxonomic situation is sharply different, however: the geographically intermediate *Constrictor* is, with respect to most characters of diagnostic value, morphologically intermediate as well. There is feasible evidence, then, in *Constrictor*, for continuity of evolutionary role which simply does not exist in *Bothrops*. I therefore regard the populations of *Constrictor* as members of a stepped-cline series demonstrating geographic variation in a single species and rank these forms as subspecifically related to each other. The first population in geographic sequence is the Tet'chien of Saint Lucia:

CONSTRICTOR CONSTRICTOR OROPHIAS (Linnaeus)

Boa orophias Linnaeus, 1758, Syst. Nat., 11: 215.

Boa diviniroqua, Duméril et Bibron, 1844, Erp. Gén., 6: 515.

Boa diviniroquax, Jan, 1864, Icon. Gén., p. 81, pl. iii.

Boa diviniroqua (part), Boulenger, 1893, Cat. Snakes, Brit. Mus., 1: 118.

Constrictor orophias (part), Stull, 1935, Proc. Boston Soc. Nat. Hist., 40(8): 405. Barbour, 1914, Mem. Mus. Comp. Zool., 44(2): 329.

Type: A specimen currently in the Museum de Geer with 280 ventrals is taken to be Linnaeus' type, *vide* Andersson (1899).

Type locality: None designated; here restricted to Praslin, Saint Lucia.

Diagnosis. A *Constrictor* with a prominent snout and a convex canthus; 65 to 75 dorsal scale rows at midbody, 270 to 288 ventrals, and 27 to 31 distinct, subrectangular, dark dorsal saddles to the level of the anus; dorsal ground color rich brown; venter white with black or grey spotting pronounced; subocular stripe distinct and complete; loreal stripe largely obsolete; dark pigment on chin and infralabials not closely corresponding to the facial stripes.

Description. In general habitus this form closely corresponds to *C. c. constrictor* of Trinidad, Tobago, and part of South America. The principal differences, aside from squamation, are in the darker dorsal coloration, increase of grey patches on the venter, and the general decomposition of the bold, regular pattern so characteristic of *C. c. constrictor*. Figures 4 and 5 show the facial markings, more prominent snout, and dorsal pattern of this form compared with those of *C. c. constrictor*.

As compared with *C. c. constrictor*, *orophias* shows an increase in the number of dark dorsal saddles, and their greater irregularity contributes to the anastomosis of some of the posterior ones. There is a decrease in number of dorsal scale rows at midbody; however, there is also an increase in number of ventrals and, with respect to this character, *orophias* is not intermediate between *constrictor* and *nebulosus* subsp. nov. of Dominica. The character, however, is far from being absolute; merely a higher average number of ventrals is not, I think, sufficient to claim that this form represents a distinct species. Nevertheless, *orophias* of Saint Lucia, not *nebulosus* subsp. nov. of Dominica, has the highest ventral counts in the genus.

Habits and habitat. Large adults are readily collected simply because of their stationary habits; a specimen seen a week, two weeks, or even a month previously is usually in the same vicinity

and easily relocated when one goes to collect it. Some, e.g. MCZ 75848, from Praslin, were said to have been using the same den sites for many years. Young specimens are very much more "as you find them"; I collected several while hunting for other things, and most often found young ones in trees — one as high as twelve meters from the ground (MCZ 75845). The Tet'chien

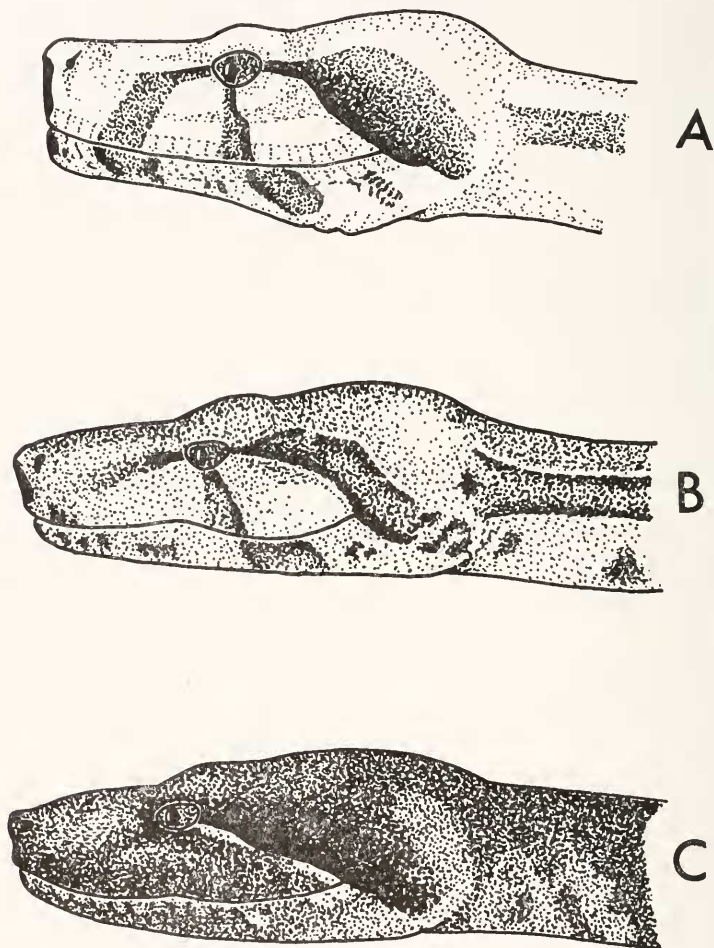


FIG. 4. Heads of three subspecies of *Constrictor constrictor*. A, *C. c. constrictor* (Linnaeus), MCZ 6105, Trinidad; B, *C. c. orophias* (Linnaeus), MCZ 74313, Praslin, Saint Lucia; C, *C. c. nebulosus* subsp. nov., Type, MCZ 65493, Woodford Hill, Dominica.

is, at any age, rather lethargic; they hiss a great deal when aroused and will strike savagely, though their accuracy leaves a good deal to be desired. They never seem to be found in the same places as *Bothrops*: for example, though I got both at Fond Citron of Grande Anse, the *Constrictor* was in uncultivated woods, the *Bothrops* in a coconut grove. Most estate owners and managers protect the Tet'chien, sometimes even fining workers for killing one; this practice is based on the belief that the Tet'chien destroys rats — which it certainly does — though probably not with anything like the efficiency of the Serpent.

Barbour (1937) claimed that the Tet'chien is "rare" on Saint Lucia; I could find no evidence of this. I never made any special attempt to find one, but rather collected them only when it was easy and convenient. The people of Saint Lucia certainly do not regard *Constrictor* as the least bit rare, though admit that they are not found in the fantastic concentrations that *Bothrops* often are. To anyone who has ever seen both a mongoose and a *Constrictor* — even a young one — the idea that mongooses could exterminate the latter must seem a shade ludicrous.

Range. The Tet'chien of Saint Lucia occupies the same region as does *Bothrops caribbaeus*, almost exactly. It does occur to higher elevations, however: *ca.* 350 meters.

Size. The largest specimen I collected, a male from Anse-La-Raye, was 2.365 meters (MCZ 75847); a female from Praslin (MCZ 75848) was 2.305 meters. Both of these are sizable snakes, but not by any means of maximum size: a considerably larger individual remains contentedly at Anse-La-Raye simply because I had no intention of either attempting to carry it out of the bush or to preserve it even if I got it out.

Relationships. The differences between this form and *C. c. constrictor* are absolute with respect to a number of characters (e.g., ventrals, dorsal saddles and loreal stripe). Were it not for the fact that the Dominican form is likewise absolutely distinct, and even more extreme *in the same direction* with respect to all characters except ventral count — so rendering *orophias* intermediate between two extremes of coloration, morphology, and geography — I would regard full species status as necessitated for this form. As it happens, however, we have a remarkable "stepped-cline" series of which *orophias* is the middle member of three steps.

Actually, in terms of color and shape of dorsal markings, *orophias* and *constrictor* are quite similar; with respect to squamation and number of dorsal markings, *orophias* is more similar

to the Dominican Tet'chien. In allusion to the extremely dark, clouded appearance of the latter form I describe it as:

CONSTRUCTOR CONSTRUCTOR NEBULOSUS subsp. nov.

Boa divinitoqua (part), Duméril and Bibron, 1844, Erp. Gén., 6: 515.

Boa divinitoqua (part), Boulenger, 1893, Cat. Snakes, Brit. Mus., 1: 118.

Constrictor orophias (part), Barbour, 1914, Mem. Mus. Comp. Zool., 44(2): 329; Stull, 1935, Proc. Boston Soc. Nat. Hist., 40(8): 405.

Type: MCZ 65493, J. D. Lazell, Jr. coll., 30 July, 1959.

Type locality: Woodford Hill, Dominica.

Diagnosis. A *Constrictor* with a prominent snout and a strikingly convex canthus; 59 to 69 dorsal scale rows at midbody, 258 to 273 ventrals, and 32 to 35 very obscure, irregular transverse markings to the level of the anus; dorsal ground color very dark, clouded, grey-brown; venter ash to slate grey, blotched and mottled with black; both loreal and subocular stripes absent, or, at most, partially indicated and largely obsolete; infralabials and chin merely grey.

Description of the type. MCZ 65493 is an adult female with 64 dorsal scale rows at midbody, and 264 ventrals. The anal is single. There are 19 supralabials on each side; there are 21 infralabials on the right, 20 on the left. Preserved, the type measures 1,438 mm, of which 172 mm are tail.

There are 33 dark transverse markings to the level of the anus; these markings are irregular in shape, not much darker than the dorsal ground color and appear almost more as mottling than actual transverse saddles. The dorsal ground color, in life, was greyish chocolate-brown. Posteriorly, the transverse markings become more distinct, black bordered and dark brown; the ground color, contrastingly, becomes yellower brown. On the tail, therefore, the pattern consists of very dark brown, black-bordered saddles set off by intervals of ochre.

The venter is ash grey anteriorly and becomes very dark—slate grey to black—posteriorly; there are irregular dark blotches along the lateral edges of the ventrals anteriorly, and these become obliterated posteriorly. The chin is entirely grey, though paler medially.

The head has a dark temporal stripe, extending from the eye to beyond the commissure of the mouth, distinctly darker-bordered along its ventral edge. In life, there was a discernible dark streak down the middle of the head. The face is paler grey, and there was, in life, a pink suffusion below the eye and on the loreal region. There are no indications of subocular or loreal stripes.

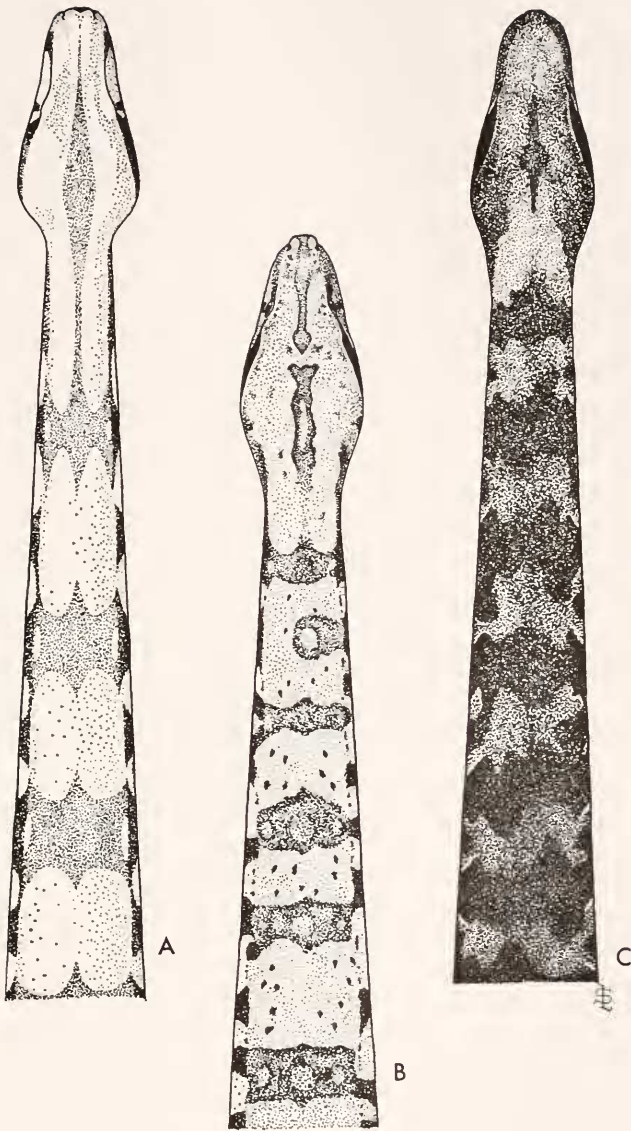


FIG. 5. Dorsal pattern in three subspecies of *Constrictor constrictor*. A, *C. c. constrictor* (Linnaeus), MCZ 6105, Trinidad; B, *C. c. orophias* (Linnaeus), MCZ 74313, Praslin, Saint Lucia; C, *C. c. nebulosus* subsp. nov., Type, MCZ 65493, Woodford Hill, Dominica.

Figure 4C shows the facial markings and Figure 5C the dorsal pattern.

Paratypes: MCZ 65494, same data as the type; MCZ 65492, Moore Park, Dominica, J. D. Lazell, Jr. coll., 21 June, 1958; MCZ 65495, Layou Park, Dominica, J. D. Lazell, Jr. coll., 14 August 1959; MCZ 58772, Trafalgar, Dominica, J. D. Lazell, Jr. coll., 18 June, 1958; MCZ 74371, Trafalgar, Dominica, J. D. Lazell, Jr. coll., 18 June, 1959; MCZ 6106, Portsmouth, Dominica, S. Garman coll., 1879.

Variation. Variation in dorsal scale rows at midbody, number of ventrals, and number of transverse markings to the level of the anus is tabulated (Table 4). Supralabials vary from 19 to 21; infralabials vary from 20 to 22.

The dorsal ground color varies somewhat, MCZ 65493 representing the light extreme (still cloudy grey-brown and with very indistinct markings), and MCZ 65492 representing the darkest individual collected (were MCZ 65492 any darker, I would be forced to call it black). MCZ 6106, collected in 1879, is pale, but this is due to fading; it is, despite this, typical in markings and shows them rather well. (A portion of a head also collected by Garman on the same trip bears the number MCZ 6107; it is deliberately not designated as a paratype.)

Habits and habitat. Barbour's (1937) comment that this form is "less uncommon" than the Tet'chien of Saint Lucia is misleading: I would describe them as being amazingly abundant. The Dominican Tet'chien, like its relative in Saint Lucia, hisses loudly when aroused and strikes rather blindly. Too, it is basically lethargic and prone to remaining in the same place for long periods of time. While staying at Woodford Hill I capitalized on their habitual laziness to save snake sacks, and merely left the snakes where I found them: they were almost always still there when I returned, even after several weeks. Congregations of three to twelve specimens denning in the same hollow log or tree stump are not at all uncommon, especially along the edges of machine-cleared banana fields where suitable den sites are often in profusion.

The people of Dominica, unlike most in Saint Lucia, have no *Bothrops* to fear and thus enjoy being deathly afraid of the Tet'chien; sometimes they even kill them, though usually only when the snakes take to raiding hen houses, which seems to be rare. Children, once initiated, are not at all afraid of even the biggest ones, however, and their parents are often shamed

into changing their minds about the danger of the Tet'chien simply because the children come to regard them as play-toys. Accidents are rare even so: even when a Tet'chien strikes with potentially dangerous accuracy, it will seldom remember to close its mouth in time to actually bite.

The Dominican *Constrictor*, like its relatives, is often encountered in trees (though large adults rarely are). Apparently they eat rats almost exclusively now, though agoutis (*Dasyproctis*) are abundant in many parts of the island and are no doubt taken as well.

Range. *Constrictor constrictor nebulosus* seems to occur throughout the island, at least to elevations of ca. 350 meters. It is, however, confined to wet ravines in dry country, e.g. at the south tip around Scott's Head, and may be largely replaced along the very dry northern leeward coast by the "Tet'chien Blanc," *Clelia*.

Size. The largest specimen collected, MCZ 65495, is a female of 1,847 mm total length; the tail is truncated, being only 87 mm long. Another female, MCZ 65492, is of more normal proportions, being 1,786 mm total length, of which 203 mm is tail. As with the Saint Lucian form, however, these specimens are far short of maximum for their taxon. A specimen owned by René Honegger of the Zurich Zoo (one of a litter produced in 1958 at the Philadelphia Zoo), is now "three meters" long (pers. comm.). For the sake of practicality, the biggest ones are best left in the bush.

Relationships. *Constrictor constrictor nebulosus* is the terminal form of a stepped-cline series, as discussed under *C. c. orophias*. Breeding experiments with other subspecies of *Constrictor constrictor* would be most interesting in assessing whether or not the subspecific rank I have accorded this form, due to its membership in a stepped-cline series, has merit from the standpoint of reproductive potential, as well as geographical and morphological characteristics. Such experiments are being contemplated by Honegger (pers. comm.), though the male he intends to use is a specimen of the very different *C. c. occidentalis*. It must be noted, however, that these two completely allopatric forms have never been subjected to any selection pressure whatever relative to interbreeding, and therefore the presence or absence of reproductive isolation between them may be entirely happenstance, if they are artificially placed in "sympatry."

DISCUSSION

In re-evaluating the taxonomy of Lesser Antillean *Bothrops* and *Constrictor* I have, in one case, separated at the species level two forms which had been previously lumped, not only with each other, but with their South American relatives; in the other case, I have split one "species" into two forms, both of which I have placed as subspecies of their South American relative. As these are island forms, I have had no possible recourse to evidence of reproductive isolation or the lack of it. It would appear also that morphological degree of difference has not been consistently used in my classification. Thus, *Bothrops caribbaeus* is absolutely different from all other members of its genus only in the characters of ventral pigmentation and dorsal pattern — color characteristics that many consider trivial, no matter how constant and definitive. *Bothrops lanceolatus*, though "more different" morphologically, is absolutely distinct ultimately only on the basis of its squamation characters combined with ventral pigmentation, thus falling back once again on a color character.

Constrictor constrictor orophias, however, is more different from any other subspecies of *Constrictor constrictor* than any of them are from each other (*nebulosus* excepted) with respect to such a conventionally respectable character as ventral count; this I have nevertheless made a subspecies. My reasons for ranking these forms as I have center around the concept of the species set forth by Simpson (1961), in which the principal criterion of conspecificity is continuity of evolutionary role.

A subspecies, as I would define it, is a rather peculiar sort of geographical variant within a species that has a wider range; it must be sharply defined (as opposed to gradually clinal) and diagnostically homogeneous (as opposed to the sort of situation which arises from discordant variation). Nevertheless, subspecies are, from the standpoint of evolutionary role, perfectly continuous with each other within their species. Continuity of evolutionary role, even between forms that are morphologically very dissimilar in many respects, can be maintained by direct intergradation and continuous gene flow. As Simpson (p. 153) points out, however, geographic isolation tends to break the continuity of evolutionary role by actually breaking the continuity of gene flow.

Therefore, I am willing to admit as geographic races of a single species only those geographically isolated forms in which there is apparent continuity of evolutionary role expressed in

the characteristics of the animals. (In the cases presented, the critical characteristics have been morphological but this is certainly not obligatory.) In *Constrictor* there is a sequential increase proceeding northward through the three populations in the following characters: scale size (= decrease in dorsal scale rows at midbody), number of transverse saddles, darkness of coloration, irregularity of pattern, obliteration of facial markings, and convexity of the canthus. On the other side of the slate is ventral count; in this case the sequence is broken and the geographically intermediate form has the highest average. Nevertheless, the balance of characters examined would seem to indicate that there is a continuity of evolutionary role, expressed in the morphology of the populations, proceeding from *Constrictor constrictor constrictor* through *Constrictor constrictor orophias* to *Constrictor constrictor nebulosus*.

In the case of the *Bothrops* populations, the geographic conditions are admirably suited for this sort of pattern, but the animals fail completely to conform in all discernible characters. Their morphological and behavioral characteristics are such that by any standard there can be no doubt that the Antillean forms are distinct species relative to each other. Assigning one or the other to subspecific rank under one of the South American forms would require an initial arbitrary choice as to which of the Antillean populations should be assigned to a South American form; a subsequent arbitrary choice would then be necessary to determine under which South American form to place the Antillean population chosen. In the end, we would be faced with the overwhelming reality that we had merged forms *merely because they were allopatric*.

Two primary objections to my criteria of continuity may be cited: first, the islands may have been populated in a way which obscures the true relationships of the animals. That is, had a distant island been the first place a new form differentiated, then a second, intermediate one colonized from that stock, and subsequently differentiated again, in each case the differentiation might have produced what would have been a stepped-cline series, had the geographic sequence been intelligible. Secondly, it is readily seen that no less than three populations are necessary before we can discern the stepped cline. That is, if Dominica and its *Constrictor* did not exist, I would have classified *orophias* as a full species, since there would have been no evidence for continuity of evolutionary role.

Both of these arguments are quite valid. It must be pointed out, however, that whenever a geographically and reproductively isolated, absolutely distinct population is classed as a subspecies (= a special sort of geographical variant within a more widespread species), this is an act of presumption. Conservatively speaking, the form qualifies as a species completely. It is only by means of strong evidence to the contrary that we may really refuse to rank it as such. As any taxonomist ultimately must admit, the relationships of an animal are not affected by our inability to discern them, but what we are able to say about them is.

ACKNOWLEDGMENTS

Roger Conant, of the Philadelphia Zoological Gardens, has unfailingly passed on to the Museum of Comparative Zoology any and all specimens collected by me that died while in his care. Arthur Greenhall was kind enough to supply authoritative information on Tobago. Ernest Williams, Museum of Comparative Zoology, provided the comparative material needed. G. G. Simpson, also of this Museum, was so good as to listen to and comment on my descriptions of the characters and distributions of the populations involved.

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TABLE 1
Variation in some characters of *Bothrops caribbaeus*.
ST. LUCIA

MCZ No.	Locality	Sex	Dorsal Rows at Midbody	Ventrals	Supralabials		Subocular Rows
					Right	Left	
4812	"St. Lucia"	♀	27	210	7	7	2
4814	"St. Lucia"	♀	27	205	7	7	2
4815	"St. Lucia"	♂	25	199	7	7	2
70166 ¹	Grande Anse	♀	27	212	7	8	2
70193	Grande Anse	♀	27	211	7	8	2
70194	Grande Anse	♀	27	203	8	7	2
70195	Grande Anse	♀	27	206	7	7	2
70196	Grande Anse	♂	25	198	7	7	2
70197	Grande Anse	♀	27	209	8	7	2
70198	Grande Anse	♀	29	205	7	7	2
70199	Grande Anse	♀	27	206	7	7	2
70200	Grande Anse	♂	25	203	7	7	2
70201	Grande Anse	♀	27	211	7	7	2
70202	Grande Anse	♀	27	203	7	7	2
70203	Grande Anse	♂	25	200	8	7	2
70204	Marquis	♀	29	205	7	7	2
70205	Praslin	♀	27	209	7	7	2
70206	Praslin	♂	25	201	7	7	2
70207	Praslin	♀	27	210	8	7	2
70208	Praslin	♂	25	198	7	7	2
70209	Praslin	♂	25	203	7	7	2
70210	Anse-La-Raye	♀	27	207	7	7	2
70211	Anse Galet	♀	27	207	8	7	2

¹MCZ 70167-92, young *ex* MCZ 70166, are not tabulated. Their counts are within the ranges indicated above.

TABLE 2
Variation in some characters of *Bothrops lanceolatus*.
MARTINIQUE

MCZ No.	Locality	Sex	Dorsal Rows at Midbody	Ventrals	Supralabials		Subocular Rows
					Right	Left	
4813	St. Pierre	♀	31	218	7	7	3
4816	St. Pierre	♀	33	225	8	7	3
4817	Morne Rouge	♂	31	221	8	8	3
75834	Gallochat	♂	29	225	7	7	2
75835	Rivière Noire	♀	31	229	7	8	3
75836	Morne Capot	♀	31	227	7	7	3
75837	Morne Capot	♀	31	230	7	7	3
75838	Morne Capot	♀	33	237	7	7	2
75839	Morne Capot	♀	33	221	7	7	2
75840	Grande Savane	♂	31	224	8	7	3
75841	Grande Savane	♀	33	230	8	8	3
60145	Grande Savane	♀	33	229	8	7	3

TABLE 3
Variation in some characters of *Constrictor constrictor orophias*.
ST. LUCIA

MCZ No.	Locality	Sex	Dorsal Rows at Midbody	Ventrals	Transverse Markings to Anus
74313	Praslin	♂	71	277	30
75842	Anse-La-Raye	♀	74	275	31
75843	Anse-La-Raye	♀	75	270	31
75844	Grande Anse	♂	71	277	29
75846	Marquis	♂	70	273	31
75847	Anse-La-Raye	♂	74	278	29
75848	Praslin	♀	74	278	31
6659	—	♂	65	288	30
6710	—	♂	68	275	27
6711	—	♂	68	275	30

TABLE 4
Variation in some characters of *Constrictor constrictor nebulosus*.
DOMINICA

MCZ No.	Locality	Sex	Dorsal Rows at Midbody	Ventrals	Transverse Markings to Anus
6106	Portsmouth	♂	66	273	32
58772	Trafalgar	♀	66	263	34
65492	Moore Park	♀	58	264	35
65493	Woodford Hill	♀	64	264	33
65494	Woodford Hill	♀	69	266	34
65495	Layou Park	♀	66	270	33
74371	Trafalgar	♂	60	266	32

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